

REVIEW / SYNTHÈSE

Comparative review of Pacific salmon survival rates

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Abstract: I collated estimates of survival from the literature for naturally reproducing populations of the five major commercially harvested species of Pacific salmon (*Oncorhynchus* spp.) and compared the mean and variability of survival across species and life-history stages. The conclusion that survival rates can be described with a lognormal distribution was extended to include both the marine and freshwater stages. Average egg–fry survival of pink (*O. gorbuscha*), chum (*O. keta*), and sockeye (*O. nerka*) salmon was similar (average 7%) but was significantly lower than that of coho salmon (*O. kisutch*, 19%). The egg–smolt survival of chinook (*O. tshawytscha*) was much higher than coho or sockeye that also rear in freshwater for similar periods (7 compared with 1–2%). No direct estimates exist for the marine survival rate of naturally spawning chinook stocks; however, from fecundity and freshwater survival data a species average of 1–2% was derived. Across all species freshwater contributes slightly more to total variation in egg–adult survival than does the ocean, and the schedule of mortality during the egg–adult interval depends on the natural history of each species.

Résumé : J'ai recueilli dans les publications des estimations du taux de survie de populations des cinq principales espèces commerciales de saumon du Pacifique (*Oncorhynchus* spp.) se reproduisant à l'état naturel et comparé la moyenne et la variabilité des taux de survie entre espèces et phases du cycle vital. La conclusion selon laquelle les taux de survie peuvent être décrits par une distribution lognormale a été élargie aux phases marine et dulcicole. Les taux de survie moyens oeuf–alevin des saumons rose (*O. gorbuscha*), keta (*O. keta*) et rouge (*O. nerka*) étaient semblables (moyenne de 7%), mais de beaucoup inférieurs à celui du saumon coho (*O. kisutch*, de 19%). Le taux de survie oeuf–saumoneau du saumon quinnat (*O. tshawytscha*) était de beaucoup supérieur à ceux des saumons coho ou rouge élevés en eau douce pendant des périodes semblables (7% comparativement à 1–2%). Nous ne disposons d'aucune quinnat qui fraient naturellement, mais les données de fécondité et de survie en eau douce permettent de déduire un taux de 1–2% pour cette espèce. Pour l'ensemble des espèces, la période en eau douce contribue légèrement plus à la variation totale du taux de survie oeuf–adulte que celle passée en mer et l'allure de la mortalité pendant la période oeuf–adulte est fonction du cycle vital de chaque espèce.

Introduction

A feature common to all fish populations is the variability associated with recruitment (Rothschild and DiNardo 1987). Pacific salmon (*Oncorhynchus* spp.) have a complex life cycle that has three major phases culminating in recruitment to the mature population: first, as eggs and alevins in the gravel of rivers and lakes, then as young juveniles in streams and lakes, and finally as older juveniles in the ocean. Variation in survival in each habitat will contribute to total recruitment variation.

Among the five major species taken in commercial fisheries, there is considerable variation in the duration of

each phase of the life cycle. For all species, reproduction and spawning usually occurs in the summer and fall months, eggs and alevins overwinter in gravel, and fry emerge the following spring. Within a month after emergence pink (*O. gorbuscha*) and chum (*O. keta*) fry migrate directly to the ocean. The fry of coho (*O. kisutch*) and sockeye (*O. nerka*) normally take up residence in streams or lakes, respectively, for a year or more before migrating to sea as larger smolts (see reviews in Groot and Margolis 1991). There are exceptions, however, as juveniles of some sockeye stocks rear in rivers and newly emerged fry of both species have been observed to migrate directly to estuaries or the ocean (e.g., Wood et al. 1987). At least three life history strategies have been identified for chinook salmon (*O. tshawytscha*), with seaward migration occurring as newly emerged fry, 3–6 month old juveniles or as yearlings (Healey 1983). During their first months at sea juvenile salmon grow quickly, but mortality is high (Parker 1962; Ricker 1976). Migration back to the spawning areas

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normally occurs after 1.5 years of ocean residence for pink and coho, and 2.5–4.5 years for the other species (excluding precocious males).

The relative importance of the two major habitat types, freshwater and ocean, for recruitment variation is unclear. Early research concentrated on the freshwater stage: the observation of the effects of flooding and freezing on the survival of incubating eggs (e.g., Wickett 1958; Gangmark and Bakkala 1960; Thorne and Ames 1987) and correlations between river flows and the abundance of coho (Neave 1949; Smoker 1955; Scarnecchia 1981) have emphasized the importance of the freshwater environment (see also Neave 1953; Hunter 1959; Foerster 1968; Larkin 1977; Kocik and Taylor 1987). More recently, however, as stock-specific catch and escapement data have accumulated, it has become apparent that marine survival is also highly variable and can make an important contribution to recruitment variation (Peterman 1981; Mathews 1984; Sinclair et al. 1988).

In this paper, I compare means, variances, and distributions of published survival rates for Pacific salmon across species and life-history stages. I also estimate the contribution of freshwater and marine habitats to total recruitment variation. Although salmon population dynamics have been under intensive investigation for many years, reviews of survival data have concentrated on specific stages or species (Wickett 1958; Hunter 1959; Foerster 1968; Ricker 1976; Peterman 1981; Mathews 1984); similarly the recent review edited by Groot and Margolis (1991), from which many of the data sources in this paper were obtained, lacks quantitative across-species comparisons. I also reexamine differences among species first considered by Neave (1948), using the much larger database that is now available.

Methods

Data collection

I collected estimates of salmon survival from the published literature and included a limited number of unpublished accounts. Because interannual variability was a key component of my analysis, only studies of 2 or more years duration were used. No attempt was made to screen the data for quality, except in cases where estimates were based on very crude or very unorthodox methodologies. Most data were categorized by life stage as either egg–fry, egg–smolt, or smolt–adult. For some other intervals (e.g., fry–smolt, fry–adult) the data are listed in the Appendix but were used in only some of the analyses.

Egg-to-fry survival rates were most commonly based on estimates of potential egg deposition (no. of females \times fecundity), and the numbers of fry emerging the following spring, usually estimated from downstream trap counts. In a few cases, the authors made adjustments for pre-spawning mortality and interannual variation in fecundity. Estimates made from redd caps or hydraulic sampling were not used because of problems of accuracy and because they do not estimate survival for the whole egg–fry period (West and Mason 1987; Young et al. 1990).

For the freshwater rearing stage, egg–smolt or fry–smolt data were collated. In most studies smolt population sizes were estimated by traps, fences, or sonar enumerations and were usually done in or near the natal lake or stream.

Thus survival during the freshwater stages did not normally include losses during migrations from the natal areas to the sea. In my analysis I partitioned the chinook data into two groups based on freshwater residency: those from stream-type populations that rear for a year or more in rivers, and a second group consisting of populations that migrate to sea as mixtures of fry, juveniles, and possibly yearling smolts. For the second group, freshwater survival is overestimated because some freshwater rearing occurred below the smolt enumeration site, frequently in mainstem river habitats.

Smolt–adult survival rates were calculated from annual estimates of smolt abundance and total adult returns (catch + escapement). The need for annual estimates of total returns precluded the use of many marine survival data from early studies, where natural and fishing mortality were inseparable. Similarly, cases where annual estimates of fishing mortality were unavailable were not used. Marine survival estimates of fish produced by spawning channels or flow-controlled streams were included with wild populations because they probably retain the life-history characteristics of the naturally reproducing population.

Statistical distribution of survival rates

The statistical distribution of salmon survival data was examined in a procedure similar to that of Peterman (1981) with the objective of testing whether survival rates in all habitats could be modelled by the lognormal distribution. I first tested whether the simple survival rates deviated from the normal distribution using the Shapiro and Wilk (1965) test for normality, as implemented in the UNIVARIATE procedure of SAS (SAS Institute Inc. 1988). I then determined if survival data were better described by the lognormal distribution, by resubmitting the data to the test of normality after being \log_e transformed. These analyses incorporate both density-dependent and density-independent sources of mortality.

To partition out variation in survival correlated with density, I followed Peterman (1981) and used the following power function:

$$Y = a X^b e^v \text{ or } Y = a X^b + v$$

where X and Y are abundance (e.g., eggs, X , and fry, Y), and b is a parameter of density dependence ($b = 1$ in the density independent case, $b < 1$ when survival decreases with increasing abundance). In the first version, where random variation, v , follows a multiplicative log-normal distribution, parameters were estimated by linear regression with the abundance estimates \log_e transformed. In the second version random noise enters in an additive normal fashion; the model was fit by nonlinear regression (SAS NLIN procedure, SAS Institute Inc. 1988). In both cases residuals from the fitted regressions were tested for normality. As Peterman (1981) has already analyzed marine survival rates, I only tested the distribution of residuals from these functions for the freshwater stages. Although the power function is a purely empirical function for modelling density dependence (Emlen et al. 1990), in the absence of a functional relationship for the density-dependent processes for each life stage, it remains a useful tool for removing the effect of density from survival data.

The Shapiro and Wilk (1965) test I used is similar in power to the Anderson–Darling statistic used by Peterman (1981; Stephens 1974). I restricted the analysis to cases with 10 or more years of data (40 of 105 cases) and caution that the power of these tests can be low for samples of less than 20 (Stephens 1974). Unfortunately less than 10% of the data sets were longer than 20 years.

Statistical analysis of mortality

Throughout the paper, survival rates are summarized by the geometric mean. All statistical tests were performed on log-transformed survival rates, because they were more normally distributed (see results below and Peterman 1981). Differences between species in stage-specific survival rates were analyzed by mixed-model ANOVA, with populations nested within species. Species was considered to be a fixed effect, and population was treated as random. Post-hoc comparisons of means were conducted with the Tukey–Kramer test, which controls α for all possible comparisons (SAS Institute Inc. 1988).

To conduct these analyses, I made some assumptions about the data. First, I ignored time-series effects that might occur within a single dataset, and treated each survival estimate as an independent observation. Although adult salmon abundance time series are sometimes significantly autocorrelated, this is most probably due to cycles in the size of the spawning populations, rather than natural mortality (Peterman 1984; Walters and Staley 1987). Autocorrelations reduce the number of degrees of freedom in the analysis; however, in the nested design I used, the tests of most interest concern the higher order effects of species and habitats. The contribution of variance components at the lowest (i.e., within population) level was small. In addition, I assumed that the survival of populations and species varied independently of each other. Although covariation in survival among species has been observed in salmon (e.g., Beacham and Starr 1982), the myriad of partial overlaps in time and space in the datasets forced me to assume that any nonindependence in the data did not play a major role in the significance tests.

I tested for differences in the interannual variability in survival among species by one-way ANOVA's conducted on the variance of log_e-transformed survival rates calculated for each population. These variance estimates were themselves log_e transformed, which, with one exception, was successful in normalizing the residuals from the ANOVA (see results). There was no overall effect of the number of years of data in each data series on the estimate of the interannual variance (ANCOVAR with stage and species as factors, $F_{1,96} = 2.39$, $P = 0.16$ for the effect of sample size on log_e-transformed variance). Therefore, the number of years of data for each population was used as a weight in the analysis, to give greater weight to longer datasets where the variance in survival would be estimated more accurately.

Components of recruitment

To check the accuracy of the data at the species level, I compared empirical estimates of mean mortality for each species to an estimate of egg–adult mortality derived from fecundity (Neave 1948; Hunter 1959; Ricker 1964). In these analyses, stage-specific mortality, M , was defined as

$-\log_e(\text{survival})$, and the mortalities for each stage were summed to an empirical estimate of total egg-to-adult mortality for the species. The second estimate of total mortality was calculated as $-\log_e(R/F)$, where R is the number of surviving female offspring and F is the number of female eggs, assumed to be half of the total fecundity. I derived two estimates of total mortality based on different values of R , the number of returning females. In the first case I assumed the population was unfished and at its carrying capacity, so that one adult female would return for each female spawner ($R = 1$). In the second, I assumed that 2.5 females would return, from which 1.5 would be harvested (i.e., a 60% sustainable exploitation rate), leaving one replacement spawner. Total mortality is higher in the first case and would most probably be due to density-dependent mortality, occurring either during spawning, or during any of the rearing stages. I expected that the empirical estimates of mortality should be closer to the fished case, as most stocks in the data base have been harvested to varying, although frequently unknown, degrees.

I estimated the relative role of freshwater and oceanic mortality in total recruitment variability by using a simple model. Survival during the egg–adult period can be represented as follows:

$$N_a = N_e S_{fw} S_{oc}$$

where the number of adults produced (N_a) is the product of the number of eggs (N_e) deposited and the survival rates for the freshwater (S_{fw}) and oceanic (S_{oc}) stages. Taking logs yields the following:

$$\log_e(N_a) = \log_e(N_e) - M_{fw} - M_{oc}$$

where M indicates total instantaneous mortality ($M = -\log_e[S]$) for each habitat. If the mortality rates vary independently of density and each other, the variance in total egg–adult mortality is as follows:

$$[1] \quad \text{Var} \{ \log_e(N_a/N_e) \} = \text{Var}(M_{fw}) + \text{Var}(M_{oc})$$

Thus from empirical estimates of the variance of M_{fw} and M_{oc} , the proportion of the total egg–adult mortality attributable to the freshwater or marine stages can be calculated by rearranging [1] above.

If mortality across the two habitats is correlated, perhaps because of the effects that large-scale climatic factors might have on both oceanic conditions and freshwater flows (Kope and Botsford 1990), a positive covariance term must be included in [1], which makes the simple allocation of sources of mortality more problematic. Similarly, if there is density-dependent freshwater or marine survival, there will be a negative covariance between freshwater and marine mortality. This will probably make a minor contribution to the variance in total egg–adult mortality as density-dependent effects usually explain only a small amount of the total variability in survival (Peterman 1982). Noting these caveats, I used equation [1] to estimate the contribution of the two habitats to variation in total egg–adult mortality.

Results

Statistical distribution of survival

The distribution of survival rates differed significantly from normal in 17 of the 40 cases that had 10 or more years of data, which is far more than expected by chance

Fig. 1. Mean and average variability of egg–fry mortality rates. Horizontal error bars are SEs of all data for each species. Mean SD is the square root of the average variance in mortality, calculated by averaging interannual variance estimates from each population, using the number of years of data for each population as a weight. Vertical bar is the SE of the mean SD; numbers beside points indicate the number of populations available for each case.

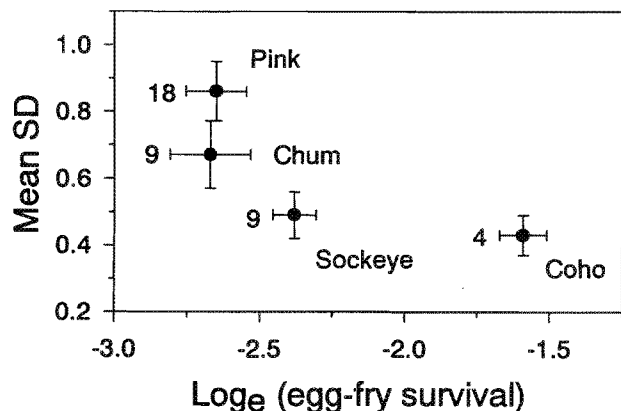
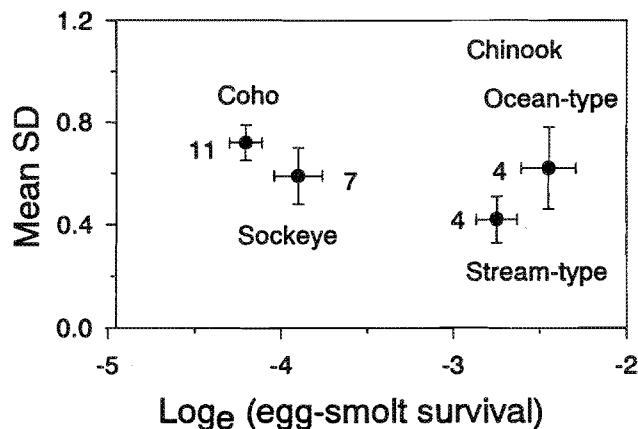


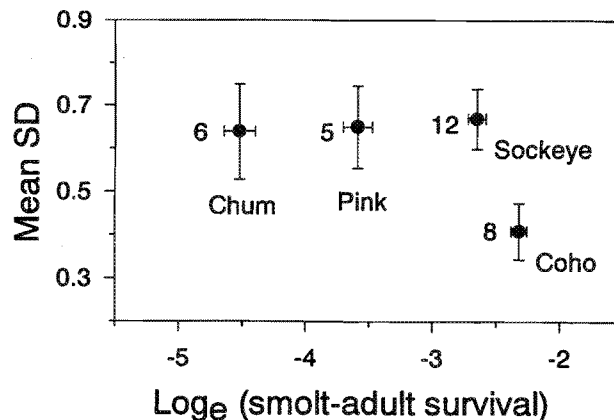
Fig. 2. Mean and variability of egg–smolt mortality rates for the freshwater rearing species; see Fig. 1 for details.



alone ($\alpha = 0.05$) under the null hypothesis of a normal distribution (Binomial test, $P < 0.001$). In contrast, only 2 of 40 were significant when survival was log transformed ($P = 0.60$). For the data from freshwater stages, 13 of 25 cases of untransformed survival rates differed from a normal distribution (more than expected by chance at $\alpha = 0.05$, $P < 0.001$). Two of 25 cases were different from normal when the data were log transformed ($P = 0.36$).

For the freshwater data, residuals from power functions were also tested for normality. Residuals from the model with an additive noise term deviated significantly from normal in 5 of 25 cases. This proportion is more than would be expected by chance at $\alpha = 0.05$ ($P = 0.007$). For the multiplicative model, 3 of 22 deviated from normal ($P = 0.13$). Thus the multiplicative model, with a log-normal noise term was slightly better at describing density-independent mortality than the additive model.

Fig. 3. Mean and variability of smolt–adult mortality rates; see Fig. 1 for details.



Comparison of survival rates

I found 326 annual estimates of egg–fry survival for 40 naturally spawning populations of chum, pink, sockeye, and coho. There was significant variation in log_e-transformed egg–fry survival among populations within species ($F_{36,286} = 4.95$, $P < 0.0001$); however, the difference among species was only marginal ($F_{3,43} = 2.79$, $P = 0.052$). Coho egg–fry survival was higher than in the other three species ($P < 0.05$; Fig. 1). Averaging across data for all species for this stage, the geometric mean survival rate from egg to emergent fry was 8.0%.

There were 246 estimates of egg–smolt survival for 26 populations of the freshwater rearing species (sockeye, coho, and chinook) in the database. The egg–smolt stage varied from 8 months to 2.5 years and included both egg incubation and freshwater rearing. I found differences both among populations within species ($F_{21,221} = 11.3$, $P < 0.0001$; Fig. 2), and among species ($F_{3,22} = 9.045$, $P = 0.0004$). Subsequent analysis with the Tukey–Kramer procedure (SAS 1988) indicated that egg–smolt survival for sockeye and coho were similar but were lower than for the two groups of chinook data ($P < 0.05$). Mean chinook egg–smolt survival was much higher (for stream type $S = 6.4\%$, ocean type $S = 8.6\%$) than either sockeye (2.0%) or coho (1.5%); however, the difference in survival between the two life history types of chinook was not significant.

Survival data for the smolt-to-adult stage for naturally reproducing stocks were available for all species except chinook. There were 31 populations and a total of 347 observations. Again, significant differences were found for populations within species ($F_{26,317} = 5.70$, $P < 0.0001$) as well as among species ($F_{3,32} = 36.4$, $P < 0.0001$). The Tukey–Kramer procedure showed that each species was different from the other ($P < 0.05$, Fig. 3). Geometric mean survival rates ranged from a low of 0.7% for chum to a high of 9.8% for coho.

Interannual variation in survival

There were differences in the interannual variance of log_e-transformed egg–fry survival rates among species ($F_{3,36} = 4.00$, $P = 0.015$; Fig. 1). Sockeye and coho egg–fry survival data were less variable than those of pink and

chum; however, the Tukey–Kramer test failed to reveal any significant pairwise comparisons. There were no differences in the interannual variability in survival among species for the egg-to-smolt interval ($F_{3,22} = 2.32$, $P = 0.10$; Fig. 2).

There was a slight difference in the interannual variability of smolt–adult survival among species for the naturally reproducing stocks ($F_{3,26} = 2.90$, $P = 0.053$). Data for coho were the least variable (Fig. 3), but this difference was not significant. Residuals from this ANOVA did not follow a normal distribution ($P = 0.008$); the square root transformation did normalize the residuals but made no difference to the outcome of the statistical tests.

Components of recruitment

Under the assumption that there is little covariation among mortality rates across habitats, the proportion of variability in total mortality accounted for by the freshwater stage varied by species:

Species	% of total mortality in freshwater	% variance in freshwater
Pink	43	64
Chum	35	52
Sockeye	58	43
Coho	64	76

To quantitatively test whether mortality was more variable in the freshwater or marine stage, log-transformed variances for the two stages were combined in a two-way ANOVA. Egg–smolt data were used as the freshwater stage for sockeye and coho, and egg–fry data were used for pink and chum salmon. Across all species, the interannual variance in mortality was greater in freshwater than marine habitats (geometric mean variance 0.54 vs. 0.33); however, this difference was not significant ($F_{1,65} = 2.71$, $P = 0.10$), nor was the interaction between species and habitat ($F_{3,65} = 2.13$, $P = 0.11$).

Discussion

Statistical distribution of survival

Overall, the notion that salmon survival rates can be modelled by a lognormal distribution seems justified. My results confirm the analysis of Peterman (1981) who found that marine survival rates are adequately described by the lognormal distribution, and I provide evidence that the same is true of survival in freshwater. Peterman (1981) and Crittenden (1993) discuss the theoretical reasons for expecting a lognormal distribution, and the consequences of this type of variation on the dynamics and productivity of salmon populations. I note, however, that in over half the data sets neither the normal nor lognormal distribution was rejected by the normality test, possibly because of low power resulting from small sample sizes. When the analysis was restricted to cases with 20 or more years of data, in five of nine cases were satisfactorily fit by either model. An alternative explanation is that some of the data follow an intermediate distribution between the lognormal

and normal forms. An intermediate distribution might result, for example, if the survival estimates were the result of a mixture of multiplicative variability in the biological processes, and additive measurement error in the estimation of abundance.

Survival, life stages, and habitats

The survival of salmon eggs and alevins in natural streams is related to the frequency of floods, droughts, and freezing in the river (Wickett 1958), the quality of the spawning gravel, and the density of spawners (reviewed by Chapman 1988). For pink, chum, and sockeye, average egg–fry survival rates were similar, ranging from 7–9%. The greater variability in pink and chum egg to fry survival resulted from the inclusion of some small coastal creeks in Alaska and B.C. (e.g., Sashin, Nile) that are subject to extreme fluctuations in flow. The unpredictability of these systems raised the mean variance for pink and chum. In contrast, the sockeye dataset included larger lake-fed systems that are probably less capricious incubation environments. Neave (1949) suggested that chum incubation survival was much lower than for pink because of the poorer spawning sites that chum occupied; however, his hypothesis was based on fewer data and is not confirmed by my analyses.

Neave (1949) found that coho egg to fry survival in tributaries of the Cowichan River, B.C., was higher than that for pink and chum salmon. He speculated that flows and incubation environments were more favourable in coho spawning areas, and that lower densities of coho spawners reduced losses because of redd superimposition. Neave's observation of higher egg-to-fry survival for coho eggs has been borne out in my data compilation, although none of his explanations have been adequately tested. Coho are known for their ability to reach small headwater streams (Sandercock 1991), which may allow them to take advantage of better spawning habitat than the other species. Actual coho egg–fry survival rates may be even higher than estimated, because, in some cases, coho fry that rear in the spawning areas or migrate upstream have not been included in the enumerations of fry emerging and migrating downstream from spawning grounds.

There appears to be an interesting contrast between the freshwater survival of coho and sockeye. Although coho egg–fry survival is relatively good, their survival as stream-rearing juveniles is less than one-third that of lake-rearing sockeye. This low survival may be related to their aggressive territorial behaviour, which, coupled with limited amounts of suitable habitat, results in the exclusion of many individuals from rearing opportunities (reviewed by Sandercock 1991). Coho produce fewer smolts per female than sockeye, but those that do survive the freshwater period have the greatest chance of living to adults of all species (Table 1). For chinook, high fecundity and good freshwater survival rates imply that far more smolts will be produced per female than for coho; however, this advantage appears to be offset by low marine survival (see below).

I found large differences in marine survival among species that was partially due to variation in life history. As noted by Parker (1962), Ricker (1962), Peterman (1981), Holtby and Scrivener (1989), and others, marine survival

Table 1. Stage-specific mean mortality (\pm SE), summarized by species.

Species	Fec	M_{unf}	M_{fsh}	M_{est}	Egg-fry	Egg-smolt	Smolt-adult
Pink	1800	6.80	5.89	6.33	2.65 \pm 0.10	—	3.68 \pm 0.12
Chum	3200	7.38	6.46	7.59	2.67 \pm 0.14	—	4.92 \pm 0.12
Sockeye	3500	7.47	6.55	6.68	2.38 \pm 0.08	3.90 \pm 0.10	2.78 \pm 0.07
Coho	3000	7.31	6.40	6.52	1.62 \pm 0.08	4.20 \pm 0.09	2.32 \pm 0.06
Chinook	4300	7.67	6.76	—	—	2.56 \pm 0.13	—

Note: Estimated mean fecundity (from Groot and Margolis 1991) was used to calculate total mortality from egg to adult based on the assumption that 1 female adult will return per spawning female (i.e., an unfished population case, M_{unf}) or assuming a return rate of 2.5 females (i.e., a sustainable exploitation rate of 60%, M_{fsh}) and a 1:1 sex ratio. M_{est} is the total mortality calculated by summing empirical data across stages. For chinook, fecundity is the mean of stocks in Table 2; the mean for the species is probably somewhat greater (Healey 1991). Sample sizes for mortality estimates range from 30 to 162.

tends to be related to both size at seaward migration and residence time in the ocean. For example, coho salmon, which migrate to sea at a relatively large average size (Randall et al. 1987) and normally spend 1.5 years (excluding jacks) at sea, have nearly twice the survival of sockeye, which are usually smaller as smolts and spend at least 1 year longer in the ocean (Foerster 1968). Pink and chum salmon, migrating as fry, have much lower marine survival than the species that smolt as yearlings (Fig. 3; see also Peterman 1981). The data also suggest that coho smolts experience less interannual variability in survival than the other species, but more information is required to statistically confirm this hypothesis.

I found, in most cases, that the species-specific egg-adult mortality estimated from the empirical database was similar to that derived from fecundity (Table 1). This suggests that the stage-specific mortality rates of Table 1 are reasonable for each species. With the exception of chum salmon, total mortality derived over all life stages were between the two mortalities (fished and unfished cases) derived from fecundity and were closer to the fished estimate, as was expected (Table 1). For chum, very high estimates of marine mortality raised total mortality above that expected by fecundity considerations alone. The average instantaneous mortality (4.92) was similar to that for Japanese hatcheries (Hiroi 1985) but was higher than other published values. Using indirect estimates of fishing mortality, Parker (1962) calculated chum marine mortality at 3.55, and Levanidov (1964, cited in Salo 1991) estimated the mortality in Russian stocks to be 3.69. These estimates appear to be low given mean fecundity. Nonetheless, chum marine mortality is probably the highest of the five species.

Importance of freshwater and ocean habitats

In all species, both freshwater and marine habitats contribute substantially to total egg-adult mortality, and both contribute roughly equally to the interannual variability in total mortality. In contrast, for Atlantic salmon (*Salmo salar*), both Chadwick (1987) and Reddin (1988) considered the freshwater stage to be relatively stable and that variation in recruitment is largely due to fluctuations in marine survival. In Pacific salmon the freshwater period is important, even for pink and chum that spend most of their life in the sea. My analysis confirms the observations of early

researchers on the importance of variation in fresh water (Wickett 1958; Hunter 1959; Larkin 1977; Skud 1981). Furthermore, the overall importance of the freshwater habitat is underestimated in my analysis because river migrations and estuary rearing are not included in my definition of the freshwater rearing period.

The relative importance of variability in freshwater and the ocean will be inaccurately estimated if there is a large difference in measurement error for freshwater and marine survival rates. Both survival rates are calculated from the same type of data: the abundance of seaward migrating smolts, and adults, either as total returns or as escape-ment. Therefore, the importance of measurement error in the estimates of the variance of survival is probably about equal and should not affect my overall conclusion that freshwater and marine habitats contribute roughly the same to recruitment variation.

Holtby and Scrivener (1989) suggested that the marine environment was more important than freshwater in coho recruitment to Carnation Creek, B.C. In their model "freshwater influences" included a number of density-dependent sources of mortality, which introduced negative covariation between egg or fry abundance and subsequent survival in freshwater. As a result, the total smolt output was relatively stable ($\text{SD of } \log_e(\text{abundance}) = 0.12$), whereas freshwater mortality alone was much more variable ($\text{SD of fry-smolt mortality} = 0.62$). Thus, for coho, although freshwater mortality is a major part of the total egg-adult mortality, variation in adult abundance might be largely due to the marine environment because smolt output is relatively constant.

Survival of chinook salmon

Fewer data are available for chinook salmon than the other species, but analysis of the data suggests some interesting differences between chinook and the other species. I found that egg-smolt survival for stream-type chinook populations was three to five times higher than for coho or sockeye populations that also spend a year or more rearing in freshwater habitats. There are a number of factors that could contribute to the higher freshwater survival of chinook. First, their large body size enables adults to spawn in larger rivers, use larger gravels, and deposit their eggs deeper in the streambed, all of which may contribute to

Table 2. Details of chinook egg-smolt mortality data used in the analysis.

Stream	Type	N	Migrant	Fec	M_{tot}	Mean M_f	Est. M_m
Cowichan R., B.C. ^a	Dam	1	Fry, 0+	4500	6.80	2.39	4.41
Fall Ck., Calif.	Nat	4	Fry, 0+	3800	6.63	2.13±0.34	4.50
John Day R., Oreg.	Nat	5	1+	4000	6.68	2.94±0.16	3.74
Lehmi R., Idaho ^b	Nat	9	Fry, 0+, 1+	4500	6.80	1.21±0.11	5.59
Qualicum R., B.C.	Flow	14	Fry, 0+	5400	6.98	2.79±0.32	4.19
Tucannon R., Wash.	Nat	4	1+	4000	6.68	2.01±0.21	4.67
Warm Springs R., Oreg. ^b	Nat	15	0+, 1+	3300	6.49	2.97±0.12	3.52
Yakima R., Wash. ^c	Dam	6	1+	4500	6.80	2.72±0.10	4.08
Yakima R., Wash. ^d	Dam	8	1+	4500	6.80	3.03±0.25	3.77

Note: Type refers to natural flow (Nat), flow controlled for fisheries purposes (Flow), or dam-regulated (Dam) discharge; *N* is the number of years of data; migrant is the life stage migrating from the study area (as newly emerged fry, 2–6 month 0+ juveniles, or 1+ yearlings migrating 1 year after emerging from the gravel); Fec is the mean fecundity; M_{tot} is the estimated total mortality assuming a sustainable harvest of 60% (see Table 1); M_f is the mean (±SE) freshwater (egg-smolt) mortality from the Appendix; M_m is the estimated marine mortality, including mortality incurred during river migrations and estuary rearing, found by subtraction. The mean of all marine mortality estimates is 4.27 ($S = 1.4\%$). Data sources are listed in the Appendix.

^aOne year of data only, not used in other analyses. Source: Lister et al. (1971).

^bAll adults are sub-2; underyearling migrants rear downstream of study area; marine mortality therefore includes some freshwater rearing.

^c1957–1961 data from Major and Mighell (1969). Values used are those adjusted by Fast et al. (1991) to standardize methodologies.

^d1981–1988 data from Fast et al. (1991).

higher egg-fry survival (Chapman 1988; Healey 1991; M.J. Bradford, unpublished data). Chinook salmon have large eggs and their newly emergent fry are the largest of the five Pacific salmon species (Beacham and Murray 1990); this may provide advantage for predator avoidance and the reduction of interspecific competitive interactions in the first months of freshwater rearing (Fowler 1972; Lister and Genoe 1970).

Chinook freshwater survival may also be high because many of the data sources are from rivers with depressed chinook stocks, which would reduce the likelihood of significant density-dependent mortality occurring during the incubation or rearing phases. The importance of this effect depends on the reduction in freshwater survival that would occur if chinook spawner densities increased to levels comparable with the coho and sockeye stocks in the database; i.e., to an exploited level of 40–60% of the unfished equilibrium levels. Simple calculations suggest that density dependence would have to be very strong to bring chinook egg-smolt survival down to the value found for coho salmon. In an extreme example, if chinook freshwater survival was halved by a doubling of spawner abundances so there was no increase in smolt production, then egg-smolt survival would still be 3–4%, well above my estimated mean for coho of 1.5%.

The marine mortality of chinook salmon, for which there are few empirical estimates, may be much higher than the other species that rear in freshwater as juveniles. I base this hypothesis on the observation that chinook are more fecund than the other species (Healey and Heard 1984) and my result that egg-smolt mortality is considerably lower for chinook than for the other freshwater rearing species. I used the method of estimating total mortality from fecundity, which was successful for the

other species, to derive marine mortality for nine chinook stocks in Table 2. The mean marine mortality for stream-type stocks was 4.07 ± 0.22 ($S = 1.7\%$), and that for the ocean or mixed strategy stocks was 4.44 ± 0.33 ($S = 1.1\%$). Marine mortality for the mixed strategy stocks is overestimated by this method because some freshwater and estuary rearing is included in the marine period. Nonetheless, the estimates of marine survival for chinook are much lower than for coho (10%) or sockeye (6%). I was able to derive an independent estimate of marine mortality for chinook salmon from Warm Springs River, Oregon, to allow a comparison with my estimate based on fecundity and freshwater mortality. Correcting adult returns to the river for an estimated average ocean and lower Columbia River fishing mortality of 24% (Lindsay et al. 1989) resulted in a marine mortality (including losses of juveniles during downstream migration and rearing in the lower river) of 3.3 ± 0.09 ($N = 11$; Waples (1991) obtained an estimate of 3.5 for this population), which is reasonably close to the predicted value of 3.52 in Table 2.

The higher marine mortality derived for chinook salmon compared with sockeye or coho is not solely the result of longer ocean residence. Most of the populations in Table 2 mature at 4 or 5 years total age and spend 2.5 or 3.5 years at sea. In their final years at sea the mortality of maturing salmon has been estimated at 0.20/year (Ricker 1976); therefore the addition of an extra 1 or 2 years to the ocean period will not make up the difference between the mortality proposed for chinook, and that observed for coho and sockeye. In addition, all of the chinook stocks in Table 2 have relatively low fecundities for this species, and the higher fecundities (up to 10 000 eggs, Healey and Heard 1984) of some populations implies that survival in freshwater or marine habitats must be much lower than those listed in Table 2.

The high mortality of wild chinook smolts in the ocean may explain why the survival to maturity of chinook smolts from hatcheries is often much less than 1% (Cross et al. 1991). For coho, the average survival of hatchery smolts is less than wild smolts (Cross et al. 1991) despite the larger than normal size at which hatchery fish are often released. If the same pattern holds for chinook salmon, and if the marine survival of wild stocks is only 1–2%, low rates of return can be expected for chinook hatcheries, which could make them a cost-ineffective method of enhancement (Winton and Hilborn 1994).

In conclusion, there are presently sufficient data to make some generalizations about the patterns of survival among the Pacific salmon species, and my analysis has revealed some unexpected differences among them. While substantial mortality occurs in the marine phase of the life cycle, the freshwater phase is sufficiently variable to contribute significantly to total recruitment variation. The observation that coho egg–fry and chinook egg–smolt survivals are higher than the other species warrants further investigation, as does my hypothesis of extremely low marine survival for chinook salmon. The interactions between mortality schedules and life histories illustrates the range of solutions that have evolved in response to selection by the various aquatic habitats that salmon utilize during their life.

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Appendix

Summary of data used in the analysis. Stages (ST) are as follows: EF, egg-fry; ES, egg-smolt; FS, fry-smolt; FA, fry-adult; SA, smolt-adult. Rep, mode of reproduction; N, natural spawning; F, flow controlled stream; S, spawning channel; *N*, number of years of data; shown is the mean (*M*) and SD of mortality.

Species	ST	Population	Rep	<i>N</i>	<i>M</i>	SD	Reference
<i>O. gorbuscha</i>	EF	Fraser R.	N	15	2.21	0.42	Pac. Sal. Comm. 1988 ^a
	EF	Harrison R.	N	5	2.36	0.65	IPSFC 1967
	EF	Hooknose Ck.	N	14	2.56	0.98	Parker 1962
	EF	Inanusi R.	N	7	2.77	0.70	Kanid'yev et al. 1970
	EE	Karymaisky Sp.	N	6	5.53	2.18	Semko 1954
	EF	Khvostovka R.	N	6	2.07	0.95	Kanid'yev et al. 1970
	EF	Lakelse Lk.	N	8	2.28	0.44	Harding 1970
	EF	Lesnaya R.	N	7	2.30	0.80	Kanid'yev et al. 1970
	EF	Lyutoga R.	N	7	2.35	0.94	
	EF	McLinton Ck.	N	6	2.03	0.48	Neave 1953
	EF	Morrison Ck.	N	2	2.88	0.25	
	EF	Nile Ck.	N	5	2.85	1.76	Wickett 1951
	EF	Okhotsk R.	N	8	2.01	0.81	Golovanov 1982
	EF	Pokosmaya R.	N	7	2.05	0.71	Kanid'yev et al. 1970
	EF	Poronay R.	N	7	1.68	0.77	
	EF	Sashin Ck.	N	25	3.36	1.50	Skud 1981
	EF	Utka R.	N	12	2.97	1.50	Gorshkov et al. 1989
	EF	Vedder R.	N	5	2.54	0.36	Chapman 1970
	SA	Fraser R.	N	15	3.51	0.51	Pac. Sal. Comm. 1988 ^a
	SA	Harrison R.	N	6	3.98	1.15	Chapman 1970
	SA	Hooknose Ck.	N	7	3.14	0.94	Hunter 1959
	SA	Lakelse Lk.	N	8	3.97	0.55	Harding 1970
	SA	Vedder R.	N	6	3.43	0.53	Chapman 1970
<i>O. keta</i>	EF	Barnes Ck.	N	4	2.24	0.65	Fedorenko and Bailey 1980
	EF	Fraser R.	N	19	2.04	0.40	Beacham and Starr 1982
	EF	Hooknose Ck.	N	14	2.57	0.98	Parker 1962
	EF	Inch Ck.	N	4	3.09	0.78	Fedorenko and Bailey 1980
	EF	Karymaisky Sp.	N	7	3.88	0.52	Semko 1954
	EF	Memu	N	3	1.35	0.41	Nagasawa and Sano 1961
	EF	Nile Ck.	N	6	4.49	1.84	Wickett 1952
	EF	Nile Ck.	F	4	2.73	0.54	
	EF	Qualicum R.	N	4	2.11	0.60	Fraser et al. 1983
	EF	Qualicum R.	F	10	1.32	0.44	
	EF	Tym' R.	N	7	2.69	0.82	Kanid'yev et al. 1970
	SA	Fraser R.	N	14	4.59	0.60	Beacham and Starr 1982
	SA	Inch Ck.	F	6	4.40	0.27	Fedorenko and Bailey 1980
	SA	Qualicum R.	N	4	5.12	0.41	Fraser et al. 1983
	SA	Qualicum R.	F	10	5.29	0.87	
<i>O. kisutch</i>	EF	Beadnell Ck.	N	4	1.39	0.41	Neave 1949
	EF	Carnation Ck.	N	15	1.63	0.54	Hartman and Scrivener 1990
	EF	Oliver Ck.	N	8	1.61	0.34	Neave 1949
	EF	Sashin Ck.	N	3	1.59	0.29	Crone and Bond 1976
	ES	Black Ck.	N	6	4.17	0.93	Nass et al. 1993, Labelle 1990
	ES	Deer Ck.	N	13	3.37	0.41	Knight 1980
	ES	Flynn Ck.	N	13	4.02	0.90	
	ES	Carnation Ck.	N	13	3.88	0.47	Hartmann and Scrivener 1990
	ES	Hunt Ck.	N	11	4.64	1.04	Fraser et al. 1983
	ES	Karymaisky Sp.	N	6	5.93	0.77	Semko 1954
	ES	Needle Br. Ck.	N	12	4.45	0.89	Knight 1980
	ES	Minter Ck.	N	11	3.79	0.83	Salo and Bayliff 1958
	ES	Nile Ck.	N	4	4.33	0.42	Wickett 1951
	ES	Qualicum R.	N	2	4.40	0.79	Fraser et al. 1983
	FA	Chilliwack R.	N	4	3.15	0.47	Schubert and Zallen 1990
	FS	Carnation Ck.	N	13	1.80	0.79	Hartman and Scrivener 1990

Appendix (concluded).

Species	ST	Population	Rep	N	M	SD	Reference
<i>O. nerka</i>	SA	Bear L.	N	20	2.99	0.66	Vincent-Lang 1992 ^b
	SA	Black Ck.	N	2	1.49	0.08	Clarke and Irvine 1989
	SA	Carnation Ck. 1+ ^c	N	17	2.12	0.52	Anderson and Scrivener 1992
	SA	Carnation Ck. 2+	N	17	1.86	0.38	
	SA	Chilliwick	N	3	1.42	0.09	Schubert and Zallen 1990
	SA	Oregon (wild)	N	26	2.49	0.41	Emlen et al. 1990
	SA	Qualicum R.	N	15	2.27	0.34	Fraser et al. 1983
	SA	Salmon R.	N	3	1.90	0.18	Schubert and Kalnin 1990
	EF	Chilko R.	N	29	2.71	0.57	Roos 1991 ^d
	EF	Fulton R.	N	4	1.77	0.42	West and Mason 1987
	EF	Fulton R.	F	18	1.74	0.41	
	EF	Karluk R.	N	8	2.20	0.49	Semko 1954
	EF	Lakelse R.	N	6	2.12	0.17	Foerster 1968
	EF	L. Pinkut Ck.	N	4	2.67	0.97	West and Mason 1987
	EF	L. Pinkut Ck.	F	18	1.62	0.43	
	EF	Six Mile Ck.	N	2	1.89	0.32	Foerster 1968
	EF	Tally Ck.	N	11	2.68	0.72	
	EF	U. Pinkut Ck.	N	9	1.69	0.33	West and Mason 1987
	EF	Williams Ck.	N	3	2.04	0.45	Foerster 1968
	ES	Babine L.	N	10	3.91	0.89	
	ES	Chilko R.	N	34	3.20	0.33	Roos 1991 ^d
	ES	Cultus L.	N	9	3.76	0.83	Foerster 1968
	ES	Dalnee L.	N	6	6.21	1.13	
	ES	Karluk R.	N	7	5.85	1.40	Semko 1954
	ES	Little Kitoi L.	N	7	3.35	0.53	Foerster 1968
	ES	Lakelse L.	N	8	4.10	0.83	
	FS	Babine R.	N	23	1.15	0.50	McDonald and Hume 1984
	FS	Chilko R.	N	26	0.72	0.31	Roos 1991 ^d
	FS	Karluk L.	N	7	3.73	1.26	Foerster 1968
	FS	Lakelse L.	N	2	1.82	0.43	
	FS	Port John L.	N	8	1.34	0.70	
	SA	Babine L.	N	24	3.43	0.68	MacDonald et al. 1987
	SA	Chilko R.	N	34	2.49	0.59	Roos 1991 ^d
	SA	Egegik R. 1+	N	7	1.93	1.00	Woolington et al. 1991
	SA	Egegik R. 2+	N	7	1.34	0.31	
	SA	Kvichak R. 1+	N	16	2.62	1.13	
	SA	Kvichak R. 2+	N	17	2.35	0.78	
	SA	Nuyakuk R. 1+	N	3	2.82	0.62	
	SA	Ugashik R. 1+	N	5	2.70	1.00	
	SA	Ugaskik R. 2+	N	6	2.51	0.94	
	SA	Washington L.	N	11	2.48	0.49	Thorne and Ames 1987
	SA	Wood R. 1+	N	14	2.74	0.35	Woolington et al. 1991
	SA	Wood R. 2+	N	14	3.19	0.98	
<i>O. tschawytsch</i>	ES	Fall Ck.	N	4	2.13	0.68	Wales and Coots 1954
	ES	John Day R.	N	5	2.94	0.36	Knox et al. 1984
	ES	Lehmi R.	N	9	1.21	0.34	Bjornn 1978
	ES	Qualicum R.	F	14	2.79	1.21	Fraser et al. 1983
	ES	Tucannon R.	N	4	2.01	0.43	Bugert et al. 1991
	ES	Warm Springs R.	N	15	2.97	0.46	Lindsay et al. 1989 ^e
	ES	Yakima R.	F	6	2.72	0.25	Major and Mighell 1969
	ES	Yakima R.	F	8	3.03	0.70	Fast et al. 1991

^aAdditional data from I. Guthrie, Pac. Salmon Comm., 1100 Robson St., Vancouver, B.C.^bD. Vincent-Lang, Alaska Dept. Fish & Game, 333 Raspberry Rd., Anchorage, AK 99518.^c1+ and 2+ refer to smolt ages.^dAdditional data from M. Henderson, DFO, 555 W. Hastings, Vancouver, BC V6B 5G3.^eAdditional data from R. Lindsay, Oregon Dept. Fish Wildl. 850 SW 15th St. Corvallis, OR 97333 and D. Olson, US Fish Wildl. Serv., 9317 Hwy 99, Vancouver, WA 98665.